Avoiding scale induced artifacts in eco–evolutionary network models

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Abstract

Ecological theory recognizes the importance of the variety of species for maintaining the functioning of ecosystems and their derived services. In this context, adaptive changes in functional traits plays a crucial role. We assert that when studying the effects of shifts in biodiversity levels using mathematical models, they must be scale–invariant, i.e., should be sensitive to the variety of species traits but not to raw species numbers. We present a testing procedure for verifying scale–invariance of eco–evolutionary network models expressed as ODEs. Furthermore, we applied our test to several influential models used for evaluating biodiversity effects on ecosystem functioning. In most of the surveyed studies the equations used failed our test. This raises doubts about the validity of previous results and calls for revisiting the theory derived from these studies. Our results foster the creation of artifact–free models, a necessary step towards building a more robust theory of ecosystem functioning.

INTRODUCTION

Few questions in ecology have received such a great attention over decades and have been so fertile in promoting research, like the one about the relation between species diversity and the functioning of ecosystems (McCann, 2000), which includes the stability of populations and communities. This is of particular concern in the context of current biodiversity loss. The importance of this matter encompasses both the theoretical understanding of ecosystems and the more pragmatic issue of conservation of ecosystem services, which are vital for human well–being. Due to the inherent complexity of ecological systems, much of these research lies on the use of mathematical models. From empirically–motivated reasoning, early ecologists (Elton, 1958) postulated a positive relation between the richness of species within communities and the dampening of perturbations as well as species persistence. This was supported by R. McArthur's work (MacArthur, 1955) and then challenged in the early 1970s by theoreticians (Gardner & Ashby, 1970; May, 1972), who showed that stability of random model communities decreased with the number of species. In the early '90s, the more general biodiversity–ecosystem functioning (BEF) paradigm emerged. It extended the concept of stability beyond that of species populations, towards aggregated ecosystem properties. Concerning biodiversity, BEF relations are driven by more than the number of species per se. For example, at a fixed number of species, different community composition of key functional traits governs resource exploitation, and species interactions (Gagic *et al.*, 2015; Aubree *et al.*, 2020). Therefore, we expect that increasing the taxonomic diversity (species richness) without modifying functional diversity (variety of functional traits) should not drive any changes in ecosystem functioning (Loreau & De Mazancourt, 2013). Moreover, functional trait composition within the community is subject to temporal changes due to ecological and adaptive dynamics. These changes are known to have a strong influence on ecosystem productivity (Cadotte

& Tucker, 2017), stability (Loreau & De Mazancourt, 2013), and resistance and tolerance to invasions (Hector *et al.*, 2001). However, the ecological perspective has been dominant for considering the BEF relation.

Recently, ecologists recognized that BEF relations are history–dependent (Valdovinos *et al.*, 2010; Aubree *et al.*, 2020). Every BEF relation is almost certainly a consequence of past community adaptation. Also, ecosystems are currently facing environmental perturbations, and their communities are constantly experiencing adaptation due to phenotypic/behavioral plasticity and genetic evolution. This imposes challenges to the way we model eco–evolutionary systems for understanding the role of species diversity in the behavior of nature. It stands to reason that proper models for studying BEF should allow us to distinguish between functional diversity and plain species richness. At the same time, said models should be able to capture temporal adaptive changes of key species traits. Besides capturing key biological features, it has been noted that ecosystem models should exhibit some fundamental forms of logical consistency (Arditi & Michalski, 1996; Kuang, 2002) that avoid artifacts on the effects of biodiversity when increasing the number of species, i.e., scale–sensitivity. This advice, which is crucial for the BEF study, has scarcely been heeded. Our literature survey, included in this paper, lists a number of influential published models of ecological networks that exhibit scale–sensitivity, as well as a few that do not. The fact that such high visibility research is liable to produce misleading results as a consequence of the mentioned artifacts highlights the need for a model design procedure that avoids scale–sensitivity pitfalls.

In this article, we will present and explain the problem of scale–sensitivity; then, we will give formal criteria to detect it in ecological network models. Therefore, if a model is being used for studying the BEF relation, especially if it includes adaptive trait dynamics, it should probably be discarded if it fails our scale–invariance criteria. We also suggest ways to fix the equations to obtain and use ecological network models that exhibit

scale–invariance. We achieve this by identifying mathematical features that introduce the scale–sensitivity and are frequently found in the ecological literature.

THE PROBLEM OF SCALE–SENSITIVITY IN ECOLOGICAL NETWORK MODELS

The usual theoretical procedure to study the BEF relation in complex ecological networks, i.e., with multiple species and trophic levels, is to conduct an *in silico* controlled experiment, as follows. First, ecological networks with different diversity levels are obtained, usually by means of an algorithm generating quasi-empirical webs such as the cascade (Cohen *et al.*, 2012) or the niche model (Williams & Martinez, 2000). Different diversity levels are most commonly obtained through varying the number of species (i.e., species richness) in the network. Second, a dynamic population model is added to each of the interacting species. Third, the model community is run for a given time lapse, after which the system stability is assessed through an appropriate measure, such as species persistence, local asymptotic stability, resilience, etc. (Pascual & Dunne, 2006). Finally, the association between species richness and stability is evaluated by visualization or statistical tools.

For evaluating the BEF relation, an essential property of ecological network models is that they must be able to capture system responses to biodiversity changes and, at the same time, they must be insensitive to spurious changes in species numbers that preserve functional diversity. For example, if we have an initial population of $x(0)$ individuals belonging to species X, but we arbitrarily *count* a fraction p of $x(0)$ (with $x_1(0) = px(0)$, see Fig. 1) as if it belonged to a species Q, and a fraction $1 - p$ of $x(0)$ (with $x_2(0) = (1 - p)x(0)$) as if it belonged to another species R, then the sum of individuals belonging to pseudo–species Q and R should behave exactly the same as the population X. In other words, artificially splitting species X into pseudo–species Q and R does not

bring any consequence for the dynamics of the community, since the behavior of $x(t)$ is exactly recovered by the behavior of $x_1(t) + x_2(t)$. Conversely, the existence of a t at which $x_1(t) + x_2(t) \neq x(t)$ would imply that a mere nominal split of X into Q and R changed the community dynamics. In this case, the model outcomes are altered by a spurious increase in the number of species, which reveals an experimental artifact in the procedure.

This artifact has a crucial importance for understanding the effects of biodiversity changes through modifying the number of functionally different species. Note that splitting a species is equivalent to adding a new species functionally identical to an existing one.

Using a model sensitive to addition of identical species will present a serious problem in the more general setting of adding functionally different species. When using such a model, if a change in the number of functionally different species is followed by alterations in the system dynamics, this result could not be attributed to functional diversity changes, since the artifactual effect of changing the number of (identical) species per se is not controlled for. Thus, a necessary condition for any model used for evaluating the consequences of biodiversity shifts is that its dynamics must not be altered by the addition of identical species. In other words, the dynamical system should be *scale–invariant*, in the following sense. Following Kondoh (2003), we will consider a system composed of a prey species of abundance P and a predator species of abundance A.

$$
\begin{aligned}
\dot{P} &= P \cdot (\rho - \beta P - \varphi \alpha A) \\
\dot{A} &= A \cdot (\sigma - \gamma A + \epsilon \varphi \alpha P)
\end{aligned}
\tag{1}
$$

The ecological interaction represented in Eq. (1) depicts the killing rate of prey by predators $\varphi \alpha A P$, with consumer preference $\alpha = 1$ since there is only a single prey species. Parameter φ is the predation rate coefficient, ϵ is the conversion efficiency of killed prey

into consumer abundance, ρ and σ are the intrinsic growth rate of preys and predators, respectively. Finally, β and γ are self–interference terms, due to intraspecific competition. All parameters are positive constants. If we increased the system's species richness by adding, for example, a new prey species while preserving the form of the model equations in Kondoh (2003), we would obtain

$$\dot{P}_1 = P_1 \cdot (\rho_1 - \beta_1 P_1 - \varphi_1 \alpha_1 A) \tag{2}$$

$$\dot{P}_2 = P_2 \cdot (\rho_2 - \beta_2 P_2 - \varphi_2 \alpha_2 A) \tag{3}$$

$$\dot{A} = A \cdot (\sigma - \gamma A + \epsilon_1 \varphi_1 \alpha_1 P_1 + \epsilon_2 \varphi_2 \alpha_2 P_2) \tag{4}$$

with predator preferences $\alpha_1 + \alpha_2 = 1$. Species P_1 and P_2 are functionally identical if and only if $\alpha_1 = \alpha_2 = 1/2$, $\rho_1 = \rho_2$, $\beta_1 = \beta_2$ and $\varphi_1 = \varphi_2$. To test whether this system is scale–invariant, let us imagine that the original prey species in Eq. (1) was *artificially* split into two new species (Eq. (2) and (3)), which are functionally identical. Biological intuition suggests that the dynamics of the $P_1 + P_2$ should be identical to the dynamics of P in Eq. (1) (Arditi & Michalski, 1996; Kuang, 2002). To obtain the dynamics of $P_1 + P_2 = P$, we simply add Eq. (2) and (3), rendering the *reduced* set of equations

$$
\begin{aligned}
\dot{P} &= P \cdot \left(\rho - \beta \frac{P}{2} - \varphi \frac{A}{2} \right) \\
\dot{A} &= A \cdot \left(\sigma - \gamma A + \epsilon \varphi \frac{P}{2} \right)
\end{aligned}
\tag{5}
$$

where $\rho = \rho_1 = \rho_2$, $\beta = \beta_1 = \beta_2$ and $\varphi = \varphi_1 = \varphi_2$. Clearly, Eq. (5) is not the same as Eq. (1). Thus, the dynamics are forced by adding new species because the model is scale–sensitive. It is easy to show that Eq. (5) presents equilibrium population densities greater than those obtained from Eq. (1).

Scale–sensitivity and BEF

Dividing a species into identical copies can affect the dynamics of the system. Now we will show that some important measures of ecosystem functioning can also be affected. Still considering model (1), assume that the predator population is divided into D identical copies. Adding the equations for these copies we obtain the reduced system

$$\dot{P} = P \cdot \left(\rho - \beta\frac{P}{D} - \varphi\frac{A}{D} \right)$$
$$\dot{A} = A \cdot \left(\sigma - \gamma A + \epsilon\varphi\frac{P}{D} \right). \tag{6}$$

Notice that D appears explicitly in the right–hand side of the equations. This immediately implies that the model is scale–sensitive. Moreover, the following ecosystem functioning metrics are also dependent on D: population equilibria, total community biomass (at equilibrium), feasibility (existence of positive equilibria), ecosystem production, community resilience and local asymptotic stability. We also analyzed a competitive system based on (6) and we obtained similar conclusions. A detailed derivation of these results can be found in Appendix S1 in Supporting Information.

SCALE–INVARIANCE CRITERIA FOR NETWORKS

We will present a test to determine if a given model is scale–invariant. To make the presentation more amenable, we will restrict our analysis to systems where each population abundance is represented by a single real variable, and the state of the system is defined only by these variables. This precludes the use of systems with stage or spatial structure, or with trait adaptation. We will extend our method to include systems with adaptation in a later section.

As we stated before, no ecological network should exhibit changes in its dynamical properties as a consequence of either increase or decrease the number of species *per*

8

se (Arditi & Michalski, 1996). Therefore, it is species *diversity*, i.e., the variety of species, not the raw number of species, what should drive changes to the system dynamics.

For this work, and given an ecological network characterized by a set of species and parameters that describe the interactions among them, we will make the following two assumptions. The first one is that there is an unambiguous procedure to translate the network into a set of ordinary differential equations (ODEs). The second one is that the operation of adding a species to a network G, yielding a network G' is defined, particularly in the case when the species added (call it s') is identical to another one (call it s) already in the network. This is conceptually equivalent to splitting the original species s in G into two identical pseudo–species s and s' in G'. Intuitively, duplicating a species should not alter the dynamics of the system since the combined population of species s and s' in G' should behave exactly like the population of s in G. More formally, given a network G, we will duplicate a species in G, yielding G', which contains s and s'. For all species i in G, the ODEs will have the form

$$\dot{x}_i = x_i \cdot f_i(\boldsymbol{x}) \tag{7}$$

with initial conditions $x_i(0)$. For G', the equations will have the form

$$\dot{\tilde{x}}_i = \tilde{x}_i \cdot \tilde{f}_i(\tilde{\boldsymbol{x}}) \tag{8}$$

and initial conditions should fulfill $\tilde{x}_s(0) + \tilde{x}_{s'}(0) = x_s(0)$, and $\tilde{x}_i(0) = x_i(0)$ for all other species. We capture the intuition of duplicating being irrelevant by demanding that for all $t > 0$

$$\tilde{x}_s(t) + \tilde{x}_{s'}(t) = x_s(t)$$
$$\tilde{x}_i(t) = x_i(t) \quad \text{for all other species} \tag{9}$$

The last two equations simply mean that the species abundances through time should

behave in exactly the same way in the G network (x_i variables) as the G' network ($\tilde{x}_i$ variables). For the particular case of species s in G, its abundance should be exactly as the added abundances of species s and s' in G'.

Defining *species addability*

Consider the model:

$$\dot{\tilde{x}}_i = \tilde{x}_i \cdot \tilde{g}_i(\tilde{x}_0, \tilde{x}_1, \ldots, \tilde{x}_n) \tag{10}$$

where the $\tilde{x}_i$'s represent the abundances of $n+1$ species and, for convenience, they are indexed from zero. We will assume the $\tilde{g}_i$ functions are "well-behaved." For example, demanding the $\tilde{g}_i$'s to be Lipschitzian is enough to guarantee the existence and uniqueness of solutions (at least locally). This form is general enough to capture most popular models in the ecological literature. Moreover, in population dynamics, it is usually the case that the existence and uniqueness of the solution extend to the $[0, \infty)$ interval.

Suppose that we identify two variables that seem to represent identical species. Since we can rename variables, without loss of generality we can assume that these two variables are $\tilde{x}_0$ and $\tilde{x}_1$. If they represented identical species, and we fixed the values for $\tilde{x}_2, \ldots, \tilde{x}_n$, then $\dot{\tilde{x}}_0 + \dot{\tilde{x}}_1$ would depend only on $\tilde{x}_0 + \tilde{x}_1$. Similarly, the values of $\dot{\tilde{x}}_2, \ldots, \dot{\tilde{x}}_n$ would depend exclusively on $\tilde{x}_0 + \tilde{x}_1$. Intuitively, if only the sum $\tilde{x}_0 + \tilde{x}_1$ matters, it is natural to combine these two variables into a new one by simple addition. More formally, we will say a function $\tilde{g}_i$ is *sum–dependent* if and only if it satisfies the following condition for all $\tilde{x}_i \geq 0$ and for all $\lambda \in [0, 1]$:

$$\tilde{g}_i(\tilde{x}_0, \tilde{x}_1, \ldots, \tilde{x}_n) = \tilde{g}_i\left(\lambda \cdot (\tilde{x}_0 + \tilde{x}_1), (1 - \lambda)(\tilde{x}_0 + \tilde{x}_1), \tilde{x}_2, \tilde{x}_3, \ldots, \tilde{x}_n\right) \tag{11}$$

An equivalent way to state the rule described in Eq. (11) is

$$\tilde{g}_i(\tilde{x}_0, \tilde{x}_1, \ldots, \tilde{x}_n) = \tilde{g}_i(\tilde{x}_0 + \beta, \tilde{x}_1 - \beta, \tilde{x}_2, \tilde{x}_3, \ldots, \tilde{x}_n) \tag{12}$$

for all non-negative $\tilde{x}_i$'s and all β's such that $0 \leq \tilde{x}_0 + \beta$ and $0 \leq \tilde{x}_1 - \beta$. Intuitively we should be able to transfer an arbitrary amount of "mass" β from species 1 to species 0 without affecting the values of any per capita effect $\tilde{g}_i$.

If the per capita growth rate of species 0 and 1 is the same, i.e.

$$\tilde{g}_0(\tilde{x}_0, \tilde{x}_1, \ldots, \tilde{x}_n) = \tilde{g}_1(\tilde{x}_0, \tilde{x}_1, \ldots, \tilde{x}_n). \tag{13}$$

and also all $\tilde{g}_i$'s are sum–dependent, we can show that $\tilde{x}_0$ and $\tilde{x}_1$ can be combined into a single variable $x_1 = \tilde{x}_0 + \tilde{x}_1$. Moreover, the resulting reduced set of equations preserves the behavior of the original system described in Eq. (10) (see Appendix S2 for details). Therefore we will say species 0 and 1 are *addable* if and only if Eq. (11) and Eq. (13) are satisfied. Concisely, if two species are addable, then we can combine them and write a reduced system. Note that we can group more than two species by using the same technique repeatedly. Thus it is enough to define addability for two species only. Yet another way of representing the property defined in Eq. (11) is

$$\frac{\partial \tilde{g}_i}{\partial \tilde{x}_0} = \frac{\partial \tilde{g}_i}{\partial \tilde{x}_1}, \tag{14}$$

assuming all $\tilde{g}_i$'s are continuously differentiable. Similarly, Eq. (13) can be written as

$$\frac{\partial \tilde{g}_0}{\partial \tilde{x}_0} = \frac{\partial \tilde{g}_1}{\partial \tilde{x}_0} \tag{15}$$

$$\frac{\partial \tilde{g}_0}{\partial \tilde{x}_1} = \frac{\partial \tilde{g}_1}{\partial \tilde{x}_1} \tag{16}$$

and demanding that $\tilde{g}_0(\tilde{x}_0, \tilde{x}_1, \ldots, \tilde{x}_n) = \tilde{g}_1(\tilde{x}_0, \tilde{x}_1, \ldots, \tilde{x}_n)$ for one point $(\tilde{x}_0, \tilde{x}_1)$. Note

that Eq. (16) can be derived from Eq. (14) and Eq. (15). To summarize this subsection, two species are addable in Eq. (10) if and only if Eq. (11) and Eq. (13) are satisfied. Alternatively, Eq. (11) can be substituted for Eq. (14) while Eq. (13) can be replaced by Eq. (15) and Eq. (16). This variety of equivalent tests can be handy, depending on what the dynamical system to be analyzed is like.

The scale–invariance test

Conceptually, the test consists of applying, for all possible networks and species in those networks, a sequence of a few steps, summarized in Fig. 2. Consider an arbitrary network G and a species s in G. Write the differential equations for all species in G. Then replace s with two identical pseudo–species we will call s_1 and s_2. This will yield a new network G'. Write the differential equations for G'. Now test for addability of s_1 and s_2 using any of the formulas given in section *Defining species addability*. If they are addable, Define $s = s_1 + s_2$ and reduce the equations. Test if the reduced equations match those written for G. A model is *scale–invariant* if, for all networks G and for all species s in G, duplicating s and then reducing the equations yields the same system as the one written for G.

[Figure 2 goes about here]

We will show two applications of the scale–invariance test. The first one is on the classic Lotka–Volterra system:

$$\dot{x}_i = x_i \cdot \left(r_i + \sum_j a_{ij} x_j \right) \tag{17}$$

Say we wish to duplicate species with index number 1 into two identical species and, therefore, with identical parameter values. Introducing variables $\tilde{x}_0$ and $\tilde{x}_1$ to represent

their abundances we obtain

$$
\begin{aligned}
\dot{\tilde{x}}_0 &= \tilde{x}_0 \cdot \left(r_1 + \sum_{j=2}^{n} a_{1,j} x_j + a_{1,1} \tilde{x}_0 + a_{1,1} \tilde{x}_1 \right) \\
\dot{\tilde{x}}_1 &= \tilde{x}_1 \cdot \left(r_1 + \sum_{j=2}^{n} a_{1,j} x_j + a_{1,1} \tilde{x}_0 + a_{1,1} \tilde{x}_1 \right) \\
\dot{\tilde{x}}_i &= x_i \cdot \left(r_i + \sum_{j=2}^{n} a_{i,j} x_j + a_{i,1} \tilde{x}_0 + a_{i,1} \tilde{x}_1 \right) \quad \text{for } i = 2, 3, \ldots, n
\end{aligned}
\tag{18}
$$

This ends the splitting part. We can easily see that Eq. (11) and Eq. (13) are satisfied by Eq. (18); therefore, species 0 and 1 are addable. Then, by creating a new variable with value $\tilde{x}_0 + \tilde{x}_1$ and reducing the equations, we obtain a system identical to Eq. (17). Since this holds for all species, we conclude that Eq. (17) is *scale–invariant*.

The second application, to show a negative example, is on Eq. (1). Copying the only plant species gives

$$
\dot{\tilde{P}}_1 = \tilde{P}_1 \cdot (\rho - \beta \tilde{P}_1 - \varphi \alpha \tilde{A})
\tag{19}
$$

$$
\dot{\tilde{P}}_2 = \tilde{P}_2 \cdot (\rho - \beta \tilde{P}_2 - \varphi \alpha \tilde{A})
\tag{20}
$$

It is immediate that the equations fulfill neither Eq. (11) nor Eq. (13). Therefore they fail our test for scale–invariance, which was expected after our analysis of Eq. (5).

Displaying the dynamical consequences of scale–sensitivity

We will show the importance of features that can determine scale–sensitivity when analyzing the BEF relation. For doing this, we will compare the long–term dynamics of four very similar models, only one of them being scale–invariant. We will start from equations

describing the dynamics of a set of plants and herbivores.

$$\dot{P}_i = r_i P_i - I_i P_i^2 - \sum_j \frac{c_{ij} A_j P_i \beta_{ij}}{1 + \beta_{ij} \sum_{k, \beta_{kj} > 0} P_k}$$

$$\dot{A}_j = q_j A_j - E_j A_j^2 + \sum_i \frac{c_{ij} A_j P_i \beta_{ij}}{1 + \beta_{ij} \sum_{k, \beta_{kj} > 0} P_k}$$

(21)

This was published, up to small notation differences, in (Thébault & Fontaine, 2010). For the scale–invariance test we assumed that if we introduced species i' as a duplicate of i, we would copy coefficient values, i.e. $r_i = r_{i'}$ and similarly for q_j, E_j, I_i, c_{ij} and β_{ij}. Our test shows that this model is scale–sensitive. The reason lies in the competition terms. To generate variants of Eq. 21, which may or may not be scale–invariant, we propose the following generalization:

$$\dot{P}_i = r_i P_i - \sum_j I_{ij} P_i P_j - \sum_j \frac{\hat{c}_{ij} A_j P_i^h \beta_{ij}^h}{1 + \beta_{ij}^h \sum_{k, \beta_{kj} > 0} P_k^h}$$

$$\dot{A}_j = q_j A_j - \sum_i E_{ij} A_i A_j + \sum_i \frac{\hat{c}_{ij} A_j P_i^h \beta_{ij}^h}{1 + \beta_{ij}^h \sum_{k, \beta_{kj} > 0} P_k^h}$$

(22)

We made three changes to Eq. (21) to obtain Eq. (22). The first one was adding terms that allow interspecific competition. The second was the incorporation of the Hill exponent h that shape the functional response. The last change is about the normalization of parameters $\hat{c}_{ij}$. We may demand that $\sum_i \hat{c}_{ij} = 1$, consistent with the constant interacting effort hypothesis (Suweis *et al.*, 2014), or we may leave them unconstrained, as in (Thébault & Fontaine, 2010). We found a scale–invariant version of Eq. (22) in which interspecific competition coefficients are not forced to zero, and $h = 1$, and the $\hat{c}_{ij}$ coefficients do not have to add up to one, i.e., are not normalized. For the scale–invariance test, in the case of normalized $\hat{c}_{ij}$'s we assumed a two step process. In the first one we copy the values, just like before. In the second one, we renormalize the coefficients so they add up to one, much like we describe more formally in section *Addability in normalized systems*.

For comparison, we run numerical simulations based on Eq. (22) (see Appendix S3 for simulation details) under four different sets of assumptions, one of them yielding our scale–invariant version. In the first treatment, we include neither interspecific competition nor $\hat{c}$'s normalization and use a Hill's exponent $h = 1$. This reproduces the results in (Thébault & Fontaine, 2010). For the second one, we include interspecific competition, we do not normalize the $\hat{c}$'s, and $h = 1$. For the third one, we include neither interspecific competition nor normalization, and $h = 1$. For the fourth treatment, we assume interspecific competition, no normalization, and $h = 2$. Only the second set of assumptions yields a scale–invariant model. We summarize the results in Fig. 3. We can observe stark differences in the responses of species persistence and biomass to changes in diversity (richness). Note that the trends in Fig. 3 A, which is based upon the model in (Thébault & Fontaine, 2010) are notoriously different from the rest of the cases. This shows that modifying a single feature that affects the scale–invariance of a model, namely competition, normalization or Hill exponent, may result in important changes to the long-term dynamics.

Scale–invariance in models with trait adaptation

It would be straightforward to generalize the results of this paper to models not captured by Eq. (10). For example, consider:

$$\dot{x}_i = x_i g_i(x_1, x_2, \ldots, x_n) + \sum_{j \neq i} x_j h_{ij}(x_1, x_2, \ldots, x_n) \tag{23}$$

We could easily extend the conditions of addability to this equation form. However, when modeling population dynamics, equations are typically expressed using per-capita growth rates as in Eq. (10). Nonetheless, some models in literature do have forms that resemble Eq. (23). For example, say x_1 and x_2 represent the respective abundances of *the same* species but in two different terrain patches. Also, assume there is migration between said

patches. Then, the model may be written as Eq. (23), see for example (McPeek & Holt, 1992). It is worthwhile to note that the test for models based on ODEs (Eq. (10)) can also be adapted to discrete–time dynamical systems (see Appendix S4).

However, Eq. (10) is not general enough to capture models with adaptation. Typically, trait adaptation is represented by adding extra variables to the model. A real variable α_{ij} may represent the preference of an individual of predator species i for prey species j. It can be a probability of attack or a fraction of time devoted to hunting that particular prey. Commonly, the values of α's are constrained. This will be important when specifying the test for species addability. If α_{ij} represents the fraction of time individuals of species i spends foraging on a resource j or a fraction of available energy allocated to a task, then we must have that $\sum_j \alpha_{ij} = 1$. This constraint must be preserved by the differential equations for all time. In this case, we say the system is *normalized*. A well known normalized model is the *replicator equation*. A *non–normalized* system is the classic *optimal diet model* (Stephens & Krebs, 1986). Here, it is only required that $0 \leq \alpha_{ij} \leq 1$, as the α's are probabilities. In this paper, we will handle both scenarios.

To represent this adaptation process, in addition to the x_i variables that model species' abundance, we introduce new variables α_{ij}. The time evolution of these new variables will be described by new equations. To simplify the notation, we will express the state variables in vector form. Then, let $\boldsymbol{x} = [x_1, x_2, \ldots, x_n]^T$. Similarly, let $\mathcal{A} = [\alpha_{ij}]$ be an $n \times n$ matrix. We will consider systems of this form:

$$
\begin{aligned}
\dot{x}_i &= x_i \cdot g_i(\boldsymbol{x}, \mathcal{A}) \\
\dot{\alpha}_{ij} &= f_{ij}(\boldsymbol{x}, \mathcal{A})
\end{aligned}
\tag{24}
$$

From this general equation, in the following sections, we will split our analysis into the non–normalized and normalized cases.

Addability in non–normalized systems

In this case we do not impose any constraints on the values for the α's. After splitting species 1 into species 0 and 1 we obtain equations of the form

$$\dot{\tilde{x}}_i = \tilde{x}_i \cdot \tilde{g}_i(\tilde{\boldsymbol{x}}, \tilde{\mathcal{A}})$$
$$\dot{\tilde{\alpha}}_{ij} = \tilde{f}_{ij}(\tilde{\boldsymbol{x}}, \tilde{\mathcal{A}}) \tag{25}$$

Note that $\tilde{\boldsymbol{x}}$ has $n + 1$ elements, while $\tilde{\mathcal{A}}$ is an $(n + 1) \times (n + 1)$ matrix. Also note that elements in $\tilde{\boldsymbol{x}}$ are indexed from zero. Rows and columns of $\tilde{\mathcal{A}}$ are also indexed form zero. For brevity, we can define $\tilde{\mathcal{F}} = [f_{ij}]$ and write Eq. (25) as

$$\dot{\tilde{x}}_i = \tilde{x}_i \cdot \tilde{g}_i(\tilde{\boldsymbol{x}}, \tilde{\mathcal{A}})$$
$$\dot{\tilde{\mathcal{A}}}_{ij} = \tilde{\mathcal{F}}(\tilde{\boldsymbol{x}}, \tilde{\mathcal{A}}) \tag{26}$$

For an arbitrary matrix M we will write $M^{(k)}$ and $M_{(k)}$ to denote the k-th column and k-th row of M respectively. Intuitively, if two species 0 and 1 are identical, their trait values for interaction with an arbitrary species j, must be the same for all time. This means that we have the time invariants $\tilde{\alpha}_{0j} = \tilde{\alpha}_{1j}$ and $\tilde{\alpha}_{i0} = \tilde{\alpha}_{i1}$. This is exactly the same as saying $\tilde{\mathcal{A}}^{(0)} = \tilde{\mathcal{A}}^{(1)}$ & $\tilde{\mathcal{A}}_{(0)} = \tilde{\mathcal{A}}_{(1)}$.

The conditions for reducing the system by adding variables $\tilde{x}_0$ and $\tilde{x}_1$ together are:

1. Initial conditions must fulfill

$$\tilde{\mathcal{A}}^{(0)}(0) = \tilde{\mathcal{A}}^{(1)}(0) \ \& \ \tilde{\mathcal{A}}_{(0)}(0) = \tilde{\mathcal{A}}_{(1)}(0) \tag{27}$$

Informally, for the two identical species their trait values for interaction with all other species must be the same at time zero.

2.

$$\forall \tilde{\boldsymbol{x}} \forall \tilde{\mathcal{A}} [\tilde{\mathcal{A}}^{(0)} = \tilde{\mathcal{A}}^{(1)} \ \& \ \tilde{\mathcal{A}}_{(0)} = \tilde{\mathcal{A}}_{(1)} \implies \tilde{g}_0(\tilde{\boldsymbol{x}}, \tilde{\mathcal{A}}) = \tilde{g}_1(\tilde{\boldsymbol{x}}, \tilde{\mathcal{A}}) \ \& \tag{28}$$

$$\tilde{\mathcal{F}}^{(0)}(\tilde{\boldsymbol{x}}, \tilde{\mathcal{A}}) = \tilde{\mathcal{F}}^{(1)}(\tilde{\boldsymbol{x}}, \tilde{\mathcal{A}}) \ \& \tag{29}$$

$$\tilde{\mathcal{F}}_{(0)}(\tilde{\boldsymbol{x}}, \tilde{\mathcal{A}}) = \tilde{\mathcal{F}}_{(1)}(\tilde{\boldsymbol{x}}, \tilde{\mathcal{A}})] \tag{30}$$

Since the $\tilde{F}^{(0)}$, $\tilde{F}^{(1)}$, $\tilde{F}_{(0)}$ and $\tilde{F}_{(1)}$ functions control the rate of change of the first two rows and columns of $\tilde{\mathcal{A}}$, we need conditions Eq. (29) and Eq. (30) to preserve the invariants. Condition Eq. (28) is analogous to Eq. (13).

3. Fixing $\tilde{\mathcal{A}}$, define $\gamma_{i,\tilde{\mathcal{A}}}(\tilde{\boldsymbol{x}}) = \tilde{g}_i(\tilde{\boldsymbol{x}}, \tilde{\mathcal{A}})$ and $\varphi_{i,j,\tilde{\mathcal{A}}}(\tilde{\boldsymbol{x}}) = f_{ij}(\tilde{\boldsymbol{x}}, \tilde{\mathcal{A}})$. The last condition is as follows:

$$\tilde{\mathcal{A}}^{(0)} = \tilde{\mathcal{A}}^{(1)} \ \& \ \tilde{\mathcal{A}}_{(0)} = \tilde{\mathcal{A}}_{(1)} \implies \gamma_{i,\tilde{\mathcal{A}}} \text{ and } \varphi_{i,j,\tilde{\mathcal{A}}} \text{ must be sum--dependent.} \tag{31}$$

This is analogous to condition Eq. (11) for systems without adaptation.

Appendix S2 shows how from the addability criteria we just described, it follows that species 0 and 1 can be combined into a single one. This results in an equation of the form Eq. (24). After this, the equation matching check must be performed.

Addability in normalized systems

Recall that a system is normalized if for adaptive trait values α_{ij} we have $\sum_j \alpha_{ij} = 1$. We have equations of the form Eq. (24) with initial conditions such that $\sum_j \alpha_{ij}(0) = 1$. We also assume that for all x_i's, $\sum_j \alpha_{ij} = 1 \implies \sum_j f_{ij}(\boldsymbol{x}, \mathcal{A}) = 0$. Therefore $\sum_j \alpha_{ij}(t) = 1$ is a dynamic invariant. A typical example is the *replicator equation*, which in our setting

would look like:

$$\dot{\alpha}_{ij} = K_i \alpha_{ij} \cdot \left(W_{ij}(\boldsymbol{x}, \mathcal{A}) - \sum_k \alpha_{ik} W_{ik}(\boldsymbol{x}, \mathcal{A}) \right) \tag{32}$$

where K_i are positive adaptation rates and W_{ij} are fitness functions. In general, as in the non-normalized case, after duplicating species 1 into species 0 and 1 we have

$$\dot{\tilde{x}}_i = \tilde{x}_i \cdot \tilde{g}_i(\tilde{\boldsymbol{x}}, \tilde{\mathcal{A}})$$
$$\dot{\tilde{\mathcal{A}}}_{ij} = \tilde{\mathcal{F}}(\tilde{\boldsymbol{x}}, \tilde{\mathcal{A}}) \tag{33}$$

In this case, duplicating species is not as straightforward as before. Simply copying the values for α's, i.e. $\tilde{\alpha}_{ij} = \alpha_{ij}$ and $\tilde{\alpha}_{0j} = \alpha_{1j}$ will ruin normalization. A reasonable rule for assigning trait values after duplicating species is

$$\tilde{\alpha}_{ij} = \frac{\alpha_{ij}}{1 + \alpha_{1j}}$$
$$\tilde{\alpha}_{0j} = \tilde{\alpha}_{1j} \tag{34}$$

This way of recomputing values for α's is nothing but replicating the values for α_{1j} and α_{i0} *and* normalizing afterwards to obtain $\sum_j \tilde{\alpha}_{ij} = 1$. This should hold in particular for $t = 0$, therefore we can compute the initial conditions for the system with duplicated species using Eq. (34). Conditions must also hold for all t. For initial conditions we have

$$\tilde{x}_i(0) = x_i(0)$$
$$\tilde{x}_0(0) + \tilde{x}_1(0) = x_1(0) \tag{35}$$

and

$$\tilde{\alpha}_{ij}(0) = \frac{\alpha_{ij}(0)}{1 + \alpha_{1j}(0)}$$
$$\tilde{\alpha}_{0j}(0) = \tilde{\alpha}_{1j}(0) \tag{36}$$

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The conditions for reducing the system by adding variables $\tilde{x}_0$ and $\tilde{x}_1$ together are:

1. Initial conditions must fulfill

$$\tilde{A}^{(0)}(0) = \tilde{A}^{(1)}(0) \ \& \ \tilde{A}_{(0)}(0) = \tilde{A}_{(1)}(0) \tag{37}$$

Informally, for the two identical species their trait values for interaction with all other species must be the same at time zero.

2.

$$\forall \tilde{x} \forall \tilde{A} [\tilde{A}^{(0)} = \tilde{A}^{(1)} \ \& \ \tilde{A}_{(0)} = \tilde{A}_{(1)} \implies \tilde{g}_0(\tilde{x}, \tilde{A}) = \tilde{g}_1(\tilde{x}, \tilde{A}) \ \& \tag{38}$$

$$\tilde{\mathcal{F}}^{(0)}(\tilde{x}, \tilde{A}) = \tilde{\mathcal{F}}^{(1)}(\tilde{x}, \tilde{A}) \ \& \tag{39}$$

$$\tilde{\mathcal{F}}_{(0)}(\tilde{x}, \tilde{A}) = \tilde{\mathcal{F}}_{(1)}(\tilde{x}, \tilde{A})] \tag{40}$$

Since the $\tilde{F}^{(0)}$, $\tilde{F}^{(1)}$, $\tilde{F}_{(0)}$ and $\tilde{F}_{(1)}$ functions control the rate of change of the first two rows and columns of $\tilde{A}$, we need conditions Eq. (39) and Eq. (40) to preserve the invariants. Condition Eq. (38) is analogous to Eq. (13).

3. Fixing $\tilde{A}$, define $\gamma_{i,\tilde{A}}(\tilde{x}) = \tilde{g}_i(\tilde{x}, \tilde{A})$ and $\varphi_{i,j,\tilde{A}}(\tilde{x}) = f_{ij}(\tilde{x}, \tilde{A})$. The last condition is as follows:

$$\tilde{A}^{(0)} = \tilde{A}^{(1)} \ \& \ \tilde{A}_{(0)} = \tilde{A}_{(1)} \implies \gamma_{i,\tilde{A}} \text{ and } \varphi_{i,j,\tilde{A}} \text{ must be sum–dependent.} \tag{41}$$

This is analogous to condition Eq. (11) for systems without adaptation.

Appendix S2 shows how from the addability criteria we just described, it follows that species 0 and 1 can be combined into a single one. This results in an equation of the form Eq. (33). After this, the equation matching check must be performed.

LITERATURE SURVEY

We surveyed the literature to find publications studying the BEF relation in ecological networks by theoretical means. These studies focus on the behavior of a community model over a gradient of species richness. Although the procedures to transform a network into a system of ODEs were straightforward, the rule to increase the number of species of a network was not always easy to deduce. Since for each reviewed model there were many possible species addition rules, we strived to chose the one that best preserves the structure of the model. Our approach was to add an equation for each added species while preserving the form of the model equations and the biological meanings of their parameters and variables. Then, we could apply our scale–invariance testing procedure. We summarize the salient properties of the models and state whether or not they are scale–invariant in the sense we define in this article. We classify the models into two main groups, those with a single state variable per species (abundance) and those with multi-variable species description to capture trait adaptation.

Ecological interaction models of a single state-variable per species

The bioenergetic model (Williams & Martinez, 2004; Brose *et al.*, 2006), which derived into the allometric trophic network model (Berlow *et al.*, 2009) is among the most widely used set of equations that represents the dynamics of foodwebs. This model is scale–sensitive because of three features it has. First, the equations incorporate intraspecific but not interspecific competition among basal species. Second, the predators' functional responses contain a Hill exponent that can assume values greater than one (in fact, it is often used with such values), and thus produce sigmoidal functions. Third, the functional responses include predator preferences that must add up to one among all prey species. Any one of these properties is enough to make it fail the test for scale–invariance described in Subsection . The model in Bascompte *et al.* (2006) is of the Lotka-Volterra type for

representing the dynamics of mutualistic ecological webs. It contains only positive interspecific interaction and includes intraspecific competition. Nonetheless, it does not contain interspecific competition, which impedes the model to pass our scale–invariance test. Later models, such as those in Okuyama & Holland (2008) which was presented to study mutualistic networks, and Thébault & Fontaine (2010) which can represent trophic as well as mutualistic interaction webs, exhibit the same problem. The model in Mougi & Kondoh (2012) represents ecological communities with different trophic and non–trophic interaction types. In this model, they include intraspecific but not interspecific competition, which makes this model to not pass our scale–invariance test. In addition, they use a normalization of interaction strength coefficient as a function of the number of neighbors, which also impedes the model to pass the test. The only one–variable per species model we could find that passes the scale–invariance test was the one in Bastolla *et al.* (2009). It is used to represent the dynamics of mutualistic networks.

Ecological interaction models with trait adaptation

The model in Kondoh (2003) represents foodweb interactions with adaptive dynamics of foraging consumer species preferences. The model fails the scale–invariance test because of two reasons. First, it does not include interspecific competition, but only intraspecific ones. Second, if i were a consumer species with a single resource, and we added $n - 1$ identical copies of that resource to the model, this would lead to a decreased total consumption rate by species i. Assuming that all resource species are identical, then the consumption term would be:

$$\frac{1}{n} e_{ij} f_{ij} \sum_{j \in resources(i)} X_j \tag{42}$$

which reveals that total consumption is n times smaller than expected from a scale–invariant model. A variant with different functional responses was published in Kondoh *et al.* (2005). This model fails the scale–invariance test because of the same two reasons

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as the one in Kondoh (2003). In this variant, after duplicating the resource species, the consumption term turns into:

$$J_i \frac{1}{n} f_{ij} \frac{\sum_{j \in i\text{'s resources}}^{n} X_j}{H_i + \frac{1}{n} \sum_{j \in i\text{'s resources}}^{n} X_j} \tag{43}$$

which reveals than total consumption decreases with the addition of identical resource species. The same class of artifact is found in Garcia-Domingo & Saldana (2007, 2008), and Guill & Drossel (2008). Hence, they are all scale–sensitive.

The model in Kondoh (2007) represents the adaptive defenses of species against their consumers, and has two alternative assumptions: a) consumer–specific defenses, and b) non–specific defenses. Both alternative models are scale–sensitive because of the lack of interspecific competition among basal species. Moreover, in model a), the dynamics are dependent on the number of species due to constraints to effort/time budgets available to defend and grow. This is similar to the problem presented in Eq. (1). This scale–sensitivity would hold even if we added interspecific competition among basals. By contrast, if we added those terms to model b), we would note two things. First, for an arbitrary species, the per capita growth rate is independent of the duplication of an interacting species. Second, the fitness gradient, which is used to define the adaptation dynamics, is also independent of duplicating species. Then, adding the competition terms would render b) scale–invariant.

The study of Uchida & Drossel (2007) describes a foodweb model in which species have adaptive behavior, allocating foraging and defense efforts. The model is scale–sensitive because of the lack of interspecific competition terms. Besides, adaptive dynamics are dependent on the number of species due to the normalization of the effort allocation coefficients f_{ij} and v_{ij}. This normalization is similar to that of the example in Eq. (1) through Eq. (5). In Uchida et $al.$ (2007), a number of foodweb models are presented. The variants without adaptive dynamics are scale–invariant. However, when they introduce

trait adaptation to the equations, the normalized trait values prevent the model from being scale–invariant. This is regardless of the type of normalization or functional response they choose.

Another approach for representing adaptive behavior is using game theory to select the trait values at a given time. In this vein, Drossel *et al.* (2001) introduce a model with foraging adaptation in which species achieve an evolutionary stable strategy. The authors affirm that their equations satisfy the logical consistency properties defined in Arditi & Michalski (1996). The adaptation model in Drossel *et al.* (2001) relies on an implicit definition of predator preference coefficients, which would be represented by the α_{ij} values in our notation. Since the changes in adaptive behavior are not represented by means of differential equations, the model is not expressed as Eq. (24). Variants of the equations were used in Drossel *et al.* (2004); McKane (2004); Quince *et al.* (2005a,b) and Powell & McKane (2008). Some models use trait values to determine coefficients in the equations. Such is the case as the eco-evolutionary model in Loeuille & Loreau (2005). This model is scale–invariant because it can be transformed into a generalized Lotka–Volterra model. The only caveat is that the rule to define the single trait associated with each species when duplicating it must be copying its value. This is analogous to the rule for non–normalized systems we described in Subsection . In Loeuille & Loreau (2005), the trait values are not used to model adaptation in the way we considered in this paper. The model can, however, be modified to do so. This was the case in Aubree *et al.* (2020), where they apply a game–theoretical approach to determine trait values, much like what is described in Drossel *et al.* (2001). The main drawback of this approach is that it requires solving a set of coupled nonlinear equations to determine the trait values every time they are needed. An approximation based on differential equations of the form Eq. (24) is proposed in Calcagno *et al.* (2017). It is not scale–invariant but can be easily transformed into one by, for example, removing the n_i factor in Eq.(22) in the Supplementary Note 2.

There are more complex models. For example, they may consider population age structure, such as Ramos-Jiliberto *et al.* (2018), which uses partial differential equations. Others represent the stage–structure of populations, such as Valdovinos *et al.* (2013, 2016). These fall beyond what can be expressed as Eq. (24) and therefore require further study.

DISCUSSION

The importance of biodiversity as a determinant of ecosystem functioning and the provision of services has been asserted before in the literature (Hooper *et al.*, 2005, 2012). This is known as the BEF relation (Gonzalez *et al.*, 2020), where biodiversity is sometimes understood as species richness. Whenever evaluating this relation through mathematical models, one should be wary about artifacts that may be introduced. In particular, for most BEF studies, we should use scale–invariant models, i.e. those that preserve system dynamics when introducing functionally identical species (Arditi & Michalski, 1996; Kuang, 2002). The key point is that even when no identical species are added, the artifacts may be still present. Whenever a scale–sensitive model is used, it is hard to discriminate between a significant BEF relation, attributable to biodiversity effects, and a spurious relation arisen from scale–sensitivity.

Hence we present a test to verify scale–invariance of ecological network models. We provide an operational definition of the test that complements Arditi and Michalski's conceptual approach to logical consistency. The procedures we describe here were successfully applied in a straightforward way to all models we cited in section *Defining species addability* as long as they were expressed as Eq. (10). Moreover, in Eq. (11) through Eq. (16), we provide alternative versions of the tests. All versions are equivalent, but some may be easier to apply than others when analyzing a particular model. As a key contribution of our study, we also present a generalized version of the test that can be applied to eco–evolutionary models, i.e., those that include trait adaptation. This feature tends to

increase stability in ecological networks, as noted in Valdovinos *et al.* (2010). To the best of our knowledge, the issue of scale–invariance in systems with adaptive trait dynamics has not been explored before. In our generalization, we considered systems in which trait values are either normalized or non-normalized. Interestingly, the tests for both cases are nearly identical. However, the procedure to add variables of identical species is more complicated in the case of normalized models due to the need for preserving the normalization of trait values. In Appendix S2 we provide the formulas describing how to write the equations after merging the duplicated species. Our approach was to describe the test to handle the renormalization rule described in Eq. (34). This rule is reasonable but somewhat arbitrary. However, the same procedure we used to derive the differential equations for the trait values, i.e., Eq. (S2.21) through Eq. (S2.26) can be used for other rules. Our test can be extended to similar models. For example, we considered equations of the form Eq. (23). These can represent populations with age or spatial structure, which has been partially explored by Kuang (2002).

To determine whether or nor an ecological network model is scale–invariant, we need unambiguous definitions for the rule to translate networks into ODEs, and for the rule to grow a network by splitting an arbitrary species into two identical ones. While surveying articles we noted that the form of the equations, and the rule to write them for a particular network were clear. Yet, the operation for duplicating species was difficult to infer. Under these conditions, it is hard to ascertain scale–invariance and, consequently, the weight of the evidence supporting BEF relations. Then, if we want to rule out the possibility of scale induced artifacts, the model specification should leave no doubts about how to add species to an existing network. This issue should be dealt with whenever presenting a model for studies aimed at determining the effects of biodiversity shifts.

As we mentioned, our survey of the literature on ecological network models showed a pervasive ambiguity in the rule to grow networks. We then had to rely on reasonable

assumptions to apply our test. Subject to these assumptions, most surveyed systems were found to be scale–sensitive. This is striking since many of those systems form the foundation of the current theory about BEF. The remarkable exceptions are in the works of Bastolla *et al.* (2009); Drossel *et al.* (2001); Loeuille & Loreau (2005) and later developments. The preponderance of scale–sensitive models undermines the development of current biodiversity theory. As a result, this may hamper the much–needed application of this theory to environmental policymaking, ecosystem management, and conservation efforts. It is worthwhile to note that the venerable Lotka–Volterra model is scale–invariant, as we showed in section *The scale–invariance test.* This formulation has been used as a starting point to create more sophisticated developments, particularly in the context of studying the effects of biodiversity. Unfortunately, many of these extensions had features that corrupted the scale–invariance. The main culprits are the lack of interspecific competition in the presence of intraspecific one, using a Hill exponent other than one, and improper use of normalized trait values in eco–evolutionary models. The replicator equation is typically used to describe the trajectory of trait values in normalized systems with trait adaptation. Neither normalization nor the replicator equation immediately implies scale–sensitivity. The way in which the normalized trait values appear in the differential equations is what causes scale–sensitivity. Scale–invariant models with normalized trait values do exist. An example of this can be found in Drossel *et al.* (2001). Although this model does not follow the form Eq. (24), it does ensure the invariant described in Eq. (9), which describes species addability. Our findings suggest the need to revisit a number of classic results in the area. For example, our experiments based on the original model by Thébault & Fontaine (2010) and our slightly modified version, which is scale–invariant, yielded qualitative differences in the relationship between species diversity and stability and biomass. Our analysis serves to identify the causes of scale–sensitivity, and it also helps to find solutions for it. Since most of the causes for scale–sensitivity of published

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models fall in the three groups mentioned before, i.e., competition, Hill exponent, and normalized trait values, it is usually easy to modify the models, so they become scale–invariant. Our approach has the advantage of providing an operational test that can directly apply to models that have the form Eq. (10) or, with more generality, Eq. (24). However, these do not cover every possible formulation found in the ecological networks literature. For example, the equations modeling adaptation found in Drossel *et al.* (2001) and in Loeuille & Loreau (2005) follow a game–theoretical approach that does not use differential equations to describe the time evolution of trait values. Instead, they assume an evolutionary stable equilibrium that has to be computed by solving an algebraic set of equations. This is conceptually similar to have an infinite rate of adaptation in our equations. For example, we could assign very large values to the K_i adaptations rates in Eq. (32). This suggests that our test could be extended to a game–theoretical adaptation model.

We address the problem of scale–invariance in models that consider time evolution. That is, we study the addability issue during the transient phase, as we describe in Eq. (9). This contrasts with the point of view in which only the stable asymptotic behavior of models matters. Such an approach may give misleading answers since many real ecosystems exhibit long phases of transient, non-equilibrium ecological dynamics (Hastings *et al.*, 2018). Although Hastings et al. refer mainly to population abundance dynamics, we could ask similar questions about trait value dynamics when there is adaptation. For example, in Drossel *et al.* (2001) and in Loeuille & Loreau (2005), it is assumed that trait values will reach equilibrium instantaneously when abundances are fixed. This is appropriate when trait values adaptation is much faster than changes in population abundance. When describing behavioral adaptation, such as modifying preferences for prey, the assumption is completely valid. However, if we consider genetic adaptation where the time scales are at least as long as those in ecological dynamics (Mustonen & Lässig, 2009),

then transient evolutionary dynamics may matter (Bisschop *et al.*, 2019).

Promising research avenues include extensions of the test in several directions of particular interest. One of them is spatial heterogeneity that affects trait and population dynamics. This problem can be addressed assuming continuous or discrete space structures. An example of the former would be the growth of biofilms; for the later, we have meta–ecosystem and classical metacommunity models. The case for single–species metapopulations has been discussed in Kuang (2002). Another possible extension useful in the context of studying the BEF would be the inclusion of age or stage structure. Again, these can be discrete, continuous, or even a combination of both (Ramos-Jiliberto *et al.*, 2018). Note that for continuous space or age structure, the preferred approach is to rely on partial differential equations, which would require to develop a more involved scale–invariance test. Another interesting aspect is considering network dynamics (Ramos-Jiliberto *et al.*, 2012). This topic is readily capturing the attention of ecologists since recent empirical long-term records of ecological networks indicate a high interaction turnover (Petanidou *et al.*, 2008; CaraDonna *et al.*, 2017; Chacoff *et al.*, 2018). In models considering additions/deletions of species and links, this could determine discontinuous changes on the value of state variables, such as populations abundances or trait values. For example, in a normalized system, if a predator reduces its diet breadth, the preferences for all the remaining preys in its diet must be renormalized. In such discrete events, scale–invariance should also be preserved.

A future research challenge is finding criteria for developing proper theoretical models that include the interplay among space heterogeneity, age/stage population structure, and network dynamics. These issues are of paramount importance in epidemiological dynamics in the framework of biodiversity–driven dilution/amplification effects on disease propagation (Civitello *et al.*, 2015; Luis *et al.*, 2018). This topic has been studied using essentially the same models and techniques as we described here but without addressing

scale–invariance (Duffy & Collins, 2019). These advances could be an important step toward a deeper understanding of the role of biodiversity in the stability and functioning of ecosystems and social-ecological systems. If we intend to achieve robust predictions about ecosystems and we admit the importance of mathematical modeling to achieve this goal (Valdovinos, 2019), then ecologists must be especially careful when formulating new models, and when interpreting model outcomes.

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Figure 1 The concept of scale–invariance. (**A**) The consumers (snails) are represented by a single population of size x that feeds on a resource (plant) of population size y. (**B**) The consumer population is artificially split into two separate variables, x_1 and x_2. Bottom plots illustrate example trajectories of the resource and consumer populations. In the plot of panel (**B**), the sum of variables x_1 and x_2 must equal the value of variable x of panel (**A**), at every time.

Figure 2 Test for scale–invariance in ecological networks. Sequence of steps for conducting our scale–invariance test.

Figure 3 Sample simulations of Eq. (22). (**A**) Hill exponent $h = 1$, no normalization of $\hat{c}$'s, no interspecific competition. (**B**) $h = 1$, no normalization, competition. (**C**) $h = 1$, normalization, competition. (**D**) $h = 2$, no normalization, competition. Black lines with green/red error areas show plant/herbivore persistences. Green/red lines with grey error areas show plant/herbivore biomasses. Mean $\pm$ 95% confidence intervals are shown.
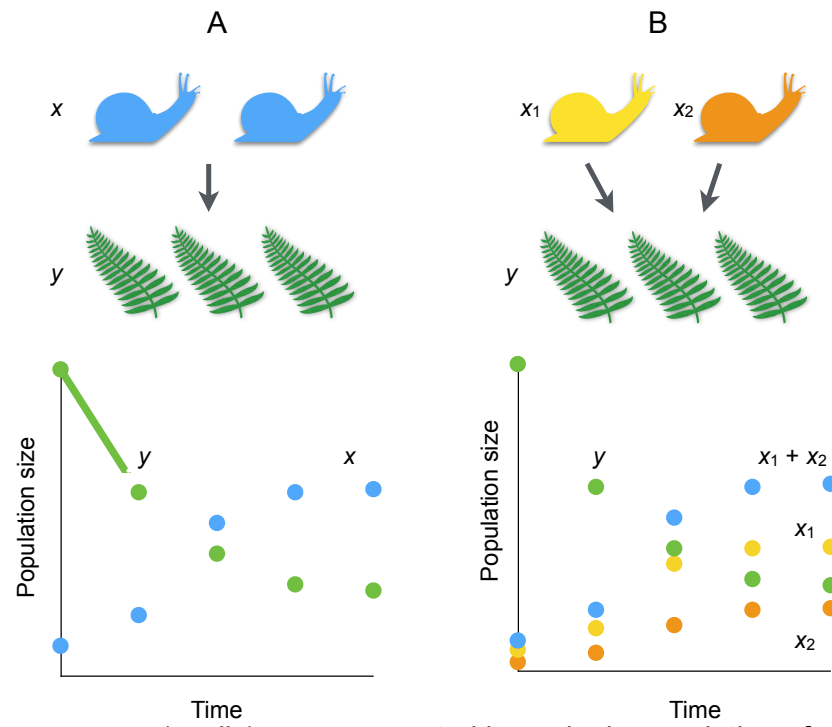
Figure 1

Figure 2

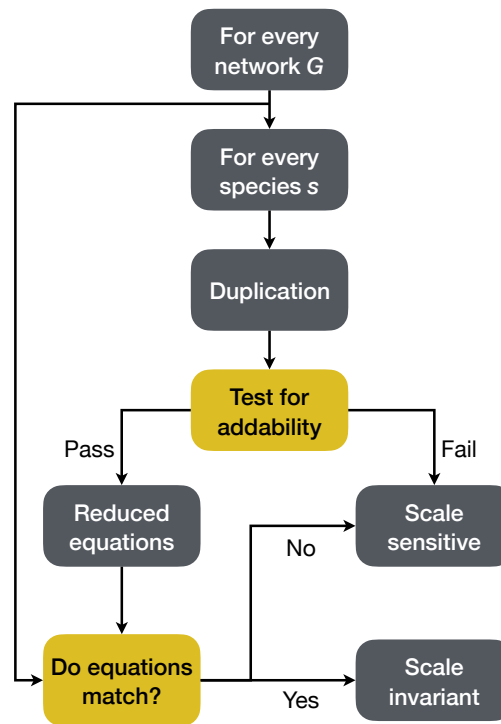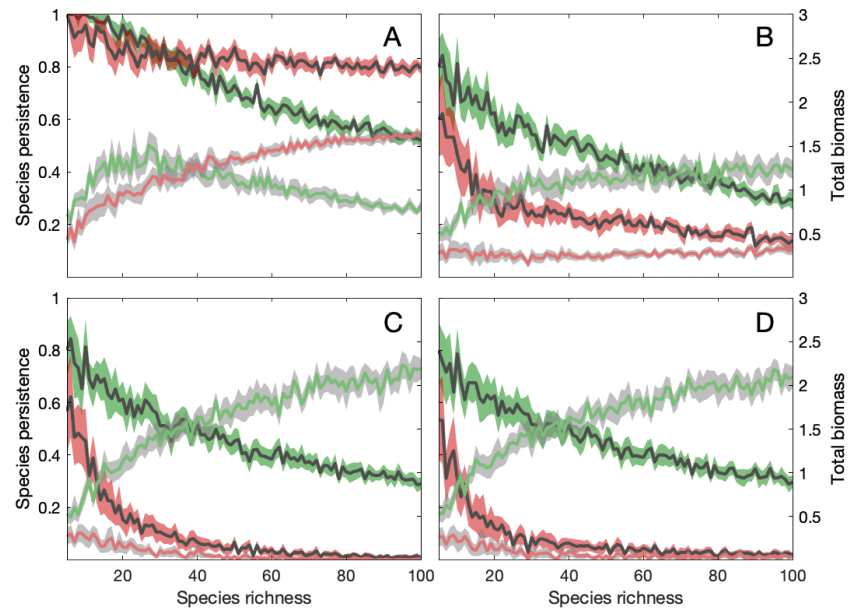**Fig. 2**

Figure 3

Fig. 3